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Predation on Juvenile *Aplysia parvula* and Other Small Anaspidean, Ascoglossan, and Nudibranch Gastropods by Pycnogonids

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Abstract. This study investigates the predation on opisthobranchs by the pycnogonid *Anoplodactylus evansi. Anoplodactylus evansi* attacked and fed on small individuals of 13 different species of anaspidean, ascoglossan (sacoglossan), and nudibranch gastropods in this study. This predator was used to investigate the feeding deterrent effects of diet-derived compounds in the sea hare *Aplysia parvula. Anoplodactylus evansi* was not deterred from feeding on *A. parvula* containing diet-derived secondary metabolites from the red seaweeds *Laurencia obtusa* or *Delisea pulchra.* However, increasing the quantity of metabolites present in *A. parvula* by treatment with adult extracts did deter *A. evansi* from feeding, suggesting that high levels of diet-derived materials in sea hares may have deterrent effects against a predator. *A. evansi* does not appear to sequester algal secondary metabolites from its prey. The abundance of *A. evansi* and *A. parvula* on the alga *L. obtusa* was measured to determine if this pycnogonid influences the population of sea hares in the field. *A. parvula* occurred in significantly lower abundance on *L. obtusa* thalli inhabited by *A. evansi* over consecutive years, a pattern consistent with population-level effects by this predator.

INTRODUCTION

Opisthobranch mollusks feed on a wide range of both macrophytes and animals, although most species have diets limited to a few prey types (Thompson et al., 1982; Paul & Pennings, 1991; Trowbridge, 1991; Rogers et al., 1995). Opisthobranchs may deter potential predators by storing noxious materials in their tissues. Such materials include chemical compounds or physical structures, which are obtained from dietary sources or produced by the animals *de novo* (Faulkner & Ghiselin, 1983; Karuso, 1987; Avila, 1995). A predator attempting to consume different species of opisthobranchs is likely to encounter a variety of defensive materials which it must overcome in order to successfully feed. The trophic flexibility required to feed on different opisthobranchs is thus probably high, and there are few reported generalist predators of these mollusks. Exceptions are some aglajid cephalaspideans which prey on other opisthobranchs (Kandel, 1979; Pennings, 1990a; Faulkner, 1992). Other predators of opisthobranchs include anemones (Nolen et al., 1995), crabs (Carefoot, 1987; Trowbridge, 1994), fishes (Pennings, 1990a; Trowbridge, 1994), seastars (Carefoot, 1987), a pycnogonid (Piel, 1991), and birds (Todd, 1981).

Ecological studies of predation on opisthobranchs have found that predator success varies, depending on opisthobranch body size (Pennings, 1990b), habitat complexity (Pennings, 1990b), and the presence of chemical defenses (Hay et al., 1989). Studies on the effects of acquired dietary compounds as defenses have mainly investigated palatability to "potential" predators. Few studies have investigated the effects on predators of different types or quantities of compounds stored by opisthobranchs. One exception is the study on sea hares by Pennings (1990b) who found that chemically depauperate *Aplysia californica* Cooper, 1863, was rejected less frequently by fishes than chemically rich conspecifics. The types and levels of defensive compounds stored by opisthobranchs may be important in determining a predator's response following contact, and so influence the outcome of an attack.

Population-level effects of predation on opisthobranchs have rarely been addressed. Sarver (1979) found high rates of mortality for juvenile *Aplysia juliana* Quoy & Gaimard, 1832, and attributed this to both abiotic and biotic factors including predators. Trowbridge (1994) used cages to exclude predators from mat-forming algae inhabited by ascoglossans in the field and found a significant difference in the abundance of the ascoglossan *Alderia modesta* Lovén, 1844, between caged and uncaged areas after 12 days. These studies suggest that rates of predation on some opisthobranchs may be high in the field, especially for small species or juveniles. In contrast, many adult opisthobranchs are generally regarded as free from predation with few reported natural enemies (Carefoot, 1987; Faulkner, 1992).

This study investigates predation on opisthobranchs by the pycnogonid *Anoplodactylus evansi* Clark, 1963. Issues addressed are:

(1) Where does *A. evansi* occur relative to opisthobranchs on a local scale?

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(2) What is the diet breadth of *A. evansi* across different sizes and species of opisthobranchs?
(3) How does the type and quantity of algal secondary metabolites stored by *Aplysia parvula* Guilding in Mörch, 1863, affect predation by this pycnogonid species?
(4) What is the abundance of *A. evansi* relative to the abundance of the sea hare *A. parvula* on the red seaweed *Laurencia obtusa* Lamouroux, 1813?

MATERIALS AND METHODS

Study Sites and Collection of Study Organisms

Collection and observation of the pycnogonid *Anoplodactylus evansi,* the sea hare *Aplysia parvula,* and the red alga *Laurencia obtusa* were done in Port Jackson, near Sydney, New South Wales (NSW), Australia, which is a warm temperate region. Four sites where *L. obtusa* occurred were used in this study (Figure 1). All four sites had sandstone reefs covered by mixed algal assemblages dominated by brown macrophytes (described by Farrant & King, 1982). *Aplysia parvula* was also collected from the red alga *Delisea pulchra* Greville, 1830, at Bare Island. The other species of opisthobranch used in this study (Table 1) were collected from the algal beds or sponge gardens on the reefs surrounding Bare Island (described by Van der Velde & King, 1984), near the entrance to Botany Bay, just south of Port Jackson. Subtidal collection of pycnogonids and opisthobranchs for experiments was done by searching algae, sponges, or other encrusting organisms *in situ,* removing the animals by hand, and placing them in a plastic container for transportation to the laboratory. Animals were held in the laboratory for observation and experiments in 10 L plastic aquaria supplied with flowing seawater, with pieces of algae (20–40 g wet weight [ww]) provided as habitat. *Anoplodactylus evansi* is reported to occur at several localities in south eastern Australia (Clark, 1963). However, this pycnogonid broods its young and does not swim, and consequently its dispersal ability is limited to movement between adjacent algae and perhaps rafting (e.g., on dislodged algae) to new habitats. All pycnogonids used in experiments were non-egg-bearing adults (leg span 20–30 mm). A voucher specimen of the pycnogonid *A. evansi* was placed with the Australian Museum in Sydney, accession number AM-P49749, the specimen being an egg-bearing adult male.

Pycnogonid Feeding

To determine the diet breadth of *Anoplodactylus evansi,* 13 species of anaspidean, ascoglossan, and nudibranch opisthobranchs, and other small invertebrates were placed in contact with adult pycnogonids held in aquaria. Opisthobranchs in a range of sizes from 50 to 820 mg (ww) were used (approximately 5–40 mm body length); the other invertebrates tested were 5–15 mm in length. Test animals were observed to determine if they were attacked by pycnogonids, and if feeding commenced. Aquaria were checked on subsequent days to determine if prey items were consumed. The method of attack and consumption by *A. evansi* was observed in aquaria, and using a dissecting microscope for prey items isolated in a glass dish. When sea hares were attacked, it was noted if ink or opaline secretion was released, and the effect this secretion had on pycnogonid behavior. Once pycnogonids had ceased feeding on sea hares, any remaining body parts were identified.

To investigate more rigorously how the capture success of pycnogonids related to prey size, individual pycnogonids and *Aplysia parvula* were weighed (ww) and placed in experimental compartments with a piece of insect mesh (1 mm) as a substratum. Predation trials were done in 25 L experimental aquaria which were partitioned into 20 separate compartments by plastic sheets. Seawater flowed through the compartments via insect mesh-covered holes before exiting into the main recirculating system. Sea hares of different size classes (< 100, 100–200, 200–300, 300–400, > 400 mg ww, $n = 35$ sea hares) were placed into contact with pycnogonids at the start of each trial. Experimental compartments were checked over the following 2 days, and the condition of each sea hare recorded.

Chemical Effects

To determine if the presence of different types of algal secondary metabolites (i.e., not from *Laurencia obtusa*) deterred *Anoplodactylus evansi* from feeding, pycnogonids were offered *Aplysia parvula* that had fed on the red seaweed *Delisea pulchra. D. pulchra* contains halogenated secondary metabolites, and *A. parvula* accumulates high concentrations of these compounds in its tissues (de Nys et al., 1996), significantly more so than *Laurencia obtusa* metabolites (Rogers et al., 2000). *D. pulchra* did not occur at the site where *A. evansi* was found, nor in that area of Port Jackson, so the secondary metabolites from this seaweed may be regarded as novel to the pycnogonids used. However, *A. evansi* would undoubtedly encounter *D. pulchra* in its wider geographic range, and consequently, pycnogonids from the study area in Port Jackson may possibly have an innate response to *D. pulchra* metabolites. Because we cannot rule out such a possibility, the term "novel" in reference to *D. pulchra* should be interpreted at the least as meaning it did not co-occur with the pycnogonids tested. Five individual pycnogonids were maintained in separate beakers and offered five replicate juvenile *A. parvula* (100–200 mg ww) collected from *D. pulchra* at Bare Island. Each sea hare was placed in contact with a pycnogonid, and the result of the trial recorded after 2 days.

To determine if increased quantities of compounds in

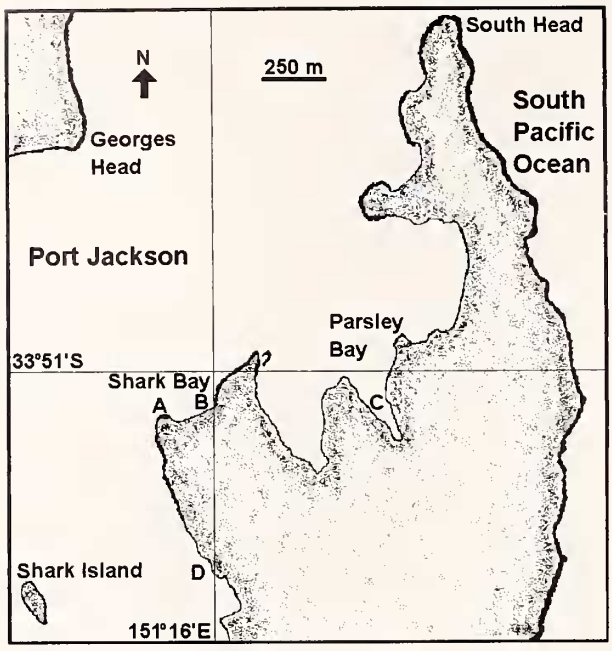

Figure 1

The position of study sites A, B, C, and D near the entrance to Port Jackson, east of Sydney, New South Wales, Australia.

sea hares deterred feeding by *Anoplodactylus evansi,* pycnogonids were held in individual cells in 25 L experimental aquaria and fed sea hares according to the following experimental design. Pycnogonids were offered either sea hares treated with adult extracts (i.e., to double the level of extract present), untreated sea hares (i.e., average levels), or solvent-treated sea hares as a control. A further group of solvent-treated sea hares was held separately in aquaria cells without pycnogonids to control for "autogenic" changes in the weight of sea hares unrelated to consumption by pycnogonids. Ten replicate animals were given each treatment. The *Aplysia parvula* used in this experiment were juveniles collected from *Delisea pulchra* (mean 123 ± SE 15 mg ww, which contain on average 4.3 ± SE 0.8 mg of non-polar extract). The juvenile sea hares were frozen, then thawed prior to use. The non-polar extract used to treat sea hares was obtained from adult *A. parvula* from *D. pulchra* by sequential extraction of freeze-dried animals, using 3 × 10 mL aliquots of dichloromethane (AR). The resulting solutions were combined, syringe filtered (PTFE 0.5 μm), then air dried. Crude extracts from sea hares contained on average 42.2 ± SE 4.5% total secondary metabolites, and juvenile and adult sea hares had similar levels of secondary metabolites in their extracts. The relationship between crude extract levels (y in mg) and sea hare wet weight (x in g) was determined for *D. pulchra* fed sea hares by linear regression ($y = 39.9 \times +0.1$, $R^2 = 0.86$, $p < 0.001$, $n = 42$). To double the quantity of extract per sea hare in the extract treatment group, the quantity of crude extract present in each juvenile sea hare was calculated, then an equivalent amount of adult extract was injected into the body cavity of the sea hare. Ethanol was the solvent used to apply the extract, and was also injected into the solvent control and autogenic control treatments at equivalent volumes to those used to administer the extract. The weight of sea hares was measured at the start of the experiment and after 2 days, and the proportional change in weight calculated.

Table 1

Opisthobranch mollusks consumed by the pycnogonid *Anoplodactylus evansi,* grouped by order and family. Published maximum lengths for each species are included (After Burn, 1989; Coleman, 1989; Wells & Bryce, 1993).

Order–Family	Species	Maximum length (mm)
Anaspidea		
Aplysiidae	*Aplysia parvula* Guilding in Mörch, 1863	60
	Aplysia dactylomela Rang, 1828	250
	Aplysia sydneyensis Sowerby, 1869	150
	Aplysia juliana Quoy & Gaimard, 1825	200
	Stylocheilus longicauda Quoy & Gaimard, 1824	40
Ascoglossa		
Oxynoidae	*Oxynoe viridis* Pease, 1861	10
Elysiidae	*Elysia australis* Quoy & Gaimard, 1832	10
Nudibranchia		
Polyceridae	*Plocamopherus imperialis* Angas, 1864	100
Chromodorididae	*Hypselodoris bennetti* Angas, 1864	50
	Glossodoris atromarginata Cuvier, 1804	50
Bornellidae	*Bornella stellifer* Adams, 1848	40
Glaucidae	*Austraeolis ornata* Angas, 1864	35
Aeolidiidae	*Spurilla australis* Rudman, 1982	55

To examine whether algal secondary metabolites are sequestered by pycnogonids after feeding, chemical analyses were done on pycnogonids that had consumed a sea hare and compared to analyses of starved pycnogonids. The *Anoplodactylus evansi* used were maintained aerated in 2 L beakers with a piece of the red alga *Laurencia obtusa* as habitat. Each treatment consisted of *Aplysia parvula* or *Aplysia dactylomela* Rang, 1828, (both collected from *L. obtusa*) or starved controls. Three replicates were given each treatment. The pycnogonids were allowed to consume the sea hares over 2 days, then were frozen for extraction. The pycnogonids were freeze dried, crushed, then sequentially extracted using 3 × 5 mL aliquots of dichloromethane (AR). The resulting extract was syringe filtered, then air dried and weighed. Samples were prepared for gas chromatography mass spectrometry (GCMS) by dissolving the extract in analytical grade ethyl acetate (0.2 mg/mL) containing 10 μg/mL naphthalene internal standard. The samples were then analyzed for *Laurencia obtusa* secondary metabolites using a Hewlett Packard HP5980 series II gas chromatograph and HP5972 mass selective detector, following the procedures of de Nys et al. (1998).

The Abundance of *Anoplodactylus evansi* and *Aplysia parvula* on *Laurencia obtusa*

The alga *Laurencia obtusa* was collected to measure the abundance of *Anoplodactylus evansi* and *Aplysia parvula* during consecutive years from three sites (A–C in Figure 1) in Port Jackson, NSW. *Laurencia obtusa* was chosen to assess the abundance of both *A. evansi* and *A. parvula* because both species were common on this alga. Algal thalli were removed from the substratum, carefully placed into individual plastic bags with seawater, and then taken to the laboratory for sorting. The number of pycnogonids and sea hares present on each thallus was recorded, and the wet weight of each thallus was measured. Sampling was commenced at site C at Parsley Bay when no *L. obtusa* were found at site B during 1996.

Statistical Analyses

Results of predation trials on different sizes of *Aplysia parvula* by *Anoplodactylus evansi* were compared in a contingency table for sea hares larger and smaller than 200 mg ww. A G-test was used to test the hypothesis that consumption of sea hares by *A. evansi* was equivalent for both size groups.

Pycnogonid consumption of extract-treated versus other *Aplysia parvula* was done using a single factor analysis of variance (ANOVA) followed by Tukey's HSD test at the $\alpha = 0.05$ significance level. Data for the proportional change in weight of sea hares were transformed using Ln(1 + x) before analysis and checked for homogeneity of variance using Cochran's test. The initial size of sea hares in each treatment was compared using a single factor ANOVA, and was not significantly different between treatments ($F_{3,39} = 2.14$, $P = 0.113$).

Field data for the size of *Laurencia obtusa* thalli, and abundance of *Aplysia parvula* were analyzed using a single factor ANOVA comparing the sites in Port Jackson, followed by Tukey's HSD test. Data for abundance of *Aplysia parvula* were Ln(1 + x) transformed. Because sites were not sampled for all dates, sampling dates were pooled for each site in comparisons. Data for abundance of *A. evansi* were not homogeneous using Cochran's test because *Anoplodactylus evansi* only occurred at one site, so a non-parametric test (Mann-Whitney) was used to compare abundance of pycnogonids between site A versus sites B and C.

RESULTS

The pycnogonid *Anoplodactylus evansi* was found only at site A in Shark Bay, Port Jackson, close to Shark Island (Figure 1) where the type specimens were collected (Clark 1963). This species was not observed at nearby sites B, C, or D (Figure 1), or at other localities in Botany Bay and Port Hacking, south of Port Jackson. The pycnogonids were found inhabiting several species of algae, including the brown algae *Sargassum linearifolium* Turner, 1809, *Sargassum vestitum* R. Brown, 1811, *Padina crassa* Yamada, 1931, *Dictyopteris acrostichoides* J. Agardh, 1882, as well as the red alga *Laurencia obtusa* and an arborescent bryozoan. Pycnogonids were observed to be nocturnally active, as were juvenile *Aplysia parvula* and *Aplysia dactylomela.* During the day, pycnogonids and sea hares were found sheltering in the basal sections of algae.

Anoplodactylus evansi consumed 13 different species of opisthobranch mollusk from eight families, encompassing three orders (Table 1). Of the species eaten, *Aplysia parvula* and the nudibranch *Bornella stellifer* Adams, 1848, were collected most often at site A where *A. evansi* occurred. *Anoplodactylus evansi* was also observed to consume an unidentified errant polychaete worm. Pycnogonids did not consume small (5–15 mm in length) amphipods, prosobranch mollusks, or echinoids that were offered to them. *A. evansi* consumed only small individuals of each opisthobranch species. Those eaten were generally less than 200 mg ww (< 10 mm in length), which for most species was much smaller than adult specimens observed in the field or published maximum sizes (Table 1) (Burn, 1989; Coleman, 1989; Wells & Bryce, 1993). When *A. evansi* was offered *A. parvula,* ranging in size from 20 to 600 mg ww, the pycnogonids could subdue and consume only animals smaller than 300 mg ww (Figure 2). The effect of prey size (< 200 versus > 200 mg ww) on consumption by *A. evansi* was significant ($G = 8.53$, $P < 0.005$). At adult size this pycnogonid species has a leg span of up to 30 mm across and weighs

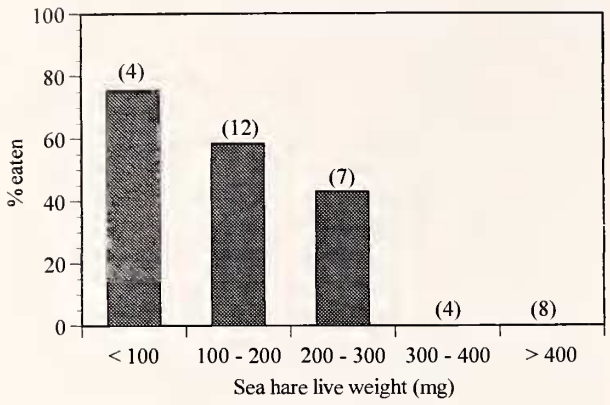

Figure 2

Consumption of different sizes of the sea hare *Aplysia parvula* by *Anoplodactylus evansi*. Bars show percentage of individuals eaten; the number of sea hares per sample is shown in brackets above the bar, (n).

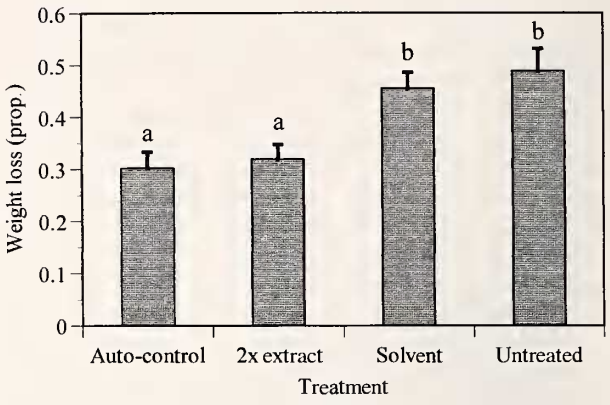

Figure 3

Mean weight loss (proportion) from *Aplysia parvula* + 1SE, for treatments offered to *Anoplodactylus evansi* (except autogenic controls). The result of a one way ANOVA on Ln(1 + x) transformed data was $F_{3,39} = 7.94$, $P < 0.01$. Treatments which are not significantly different in weight loss at $\alpha = 0.05$ using Tukey's test share the same letters on the graph. n = 10 per treatment.

50–80 mg ww. *A. evansi* feeding on 300 mg sea hares is attacking prey five to six times its own body weight.

Anoplodactylus evansi subdues prey using the front four legs to grasp and hold, while the back four legs remain secured to the substratum. Each leg ends with a long claw, which can be clamped against an opposing clawed palm, giving the pycnogonid a secure hold on slimy opisthobranchs. Once a prey item is held, *A. evansi* uses its chelicerae to tear pieces of flesh from the prey, which are passed to the proboscis, or alternatively, the proboscis is applied directly to the prey. While *A. evansi* typically consumed all of the soft tissue, some sea hare digestive glands were not consumed (33% of cases, n = 18). Sea hares often released ink when attacked, although the crouching pycnogonid was generally well clear of any secretions. Sea hare secretions did sometimes contact a front leg, and pycnogonids responded to such contact by vigorously waving the affected limb, as though irritated. Where pycnogonids were held together in the same holding tank it was noted that they would feed in groups on a prey item.

In the trial to determine if sea hares that had fed on a "novel" algae (*Delisea pulchra*) would be consumed, *Anoplodactylus evansi* ate all five juvenile *Aplysia parvula* from *D. pulchra* that were offered. However, *A. evansi* was deterred from feeding on *A. parvula* that had artificially increased levels of secondary metabolites (Figure 3). Pycnogonid feeding was significantly less on sea hares that had double extract levels compared to either solvent-treated or untreated sea hares (Figure 3). The sea hares treated with adult extract had similar weight loss to the autogenic control animals which were kept separately, without pycnogonids indicating that little, if any, feeding occurred.

Pycnogonids which had fed on *Aplysia parvula* or *A. dactylomela* containing *Laurencia obtusa* secondary metabolites contained trace amounts of the terpene palisadin A at levels below the quantitative limit of the GCMS. Such small quantities of this secondary metabolite could be attributed to sea hare tissue in the pycnogonids' gut or to low levels of accumulation. Pycnogonids which were starved as controls contained no detectable peaks for *L. obtusa* secondary metabolites on chromatographs of samples.

Collections of the red alga *Laurencia obtusa* at three sites (A–C in Figure 1) during late summer/autumn from 1995 to 1998 had significantly lower abundances of the sea hare *Aplysia parvula* on thalli where *Anoplodactylus evansi* occurred (Figure 4, Table 2). There was no significant difference between sites in the size of thalli collected (Figure 4a, Table 2). *L. obtusa* thalli at site A were observed to persist during the winter, whereas thalli at the other sites disappeared. *A. evansi* occurred only at site A. The abundance data for *A. evansi* were not homogeneous using Cochran's test, so a Mann-Whitney test with normal approximation was used to compare the abundance of pycnogonids between sites (A vs. B and C). The result was a significant difference in pycnogonid abundance between site A versus sites B and C ($Z = 6.23$, $P < 0.001$).

DISCUSSION

Anoplodactylus evansi is a generalist predator of small opisthobranchs, and other soft-bodied invertebrates, as are other *Anoplodactylus* spp. (King, 1973; Piel, 1991). This pycnogonid hunts opisthobranchs on benthic algae, immobilizing them with movable claws on the front legs, before consuming them. *A. evansi* consumed whole opis-

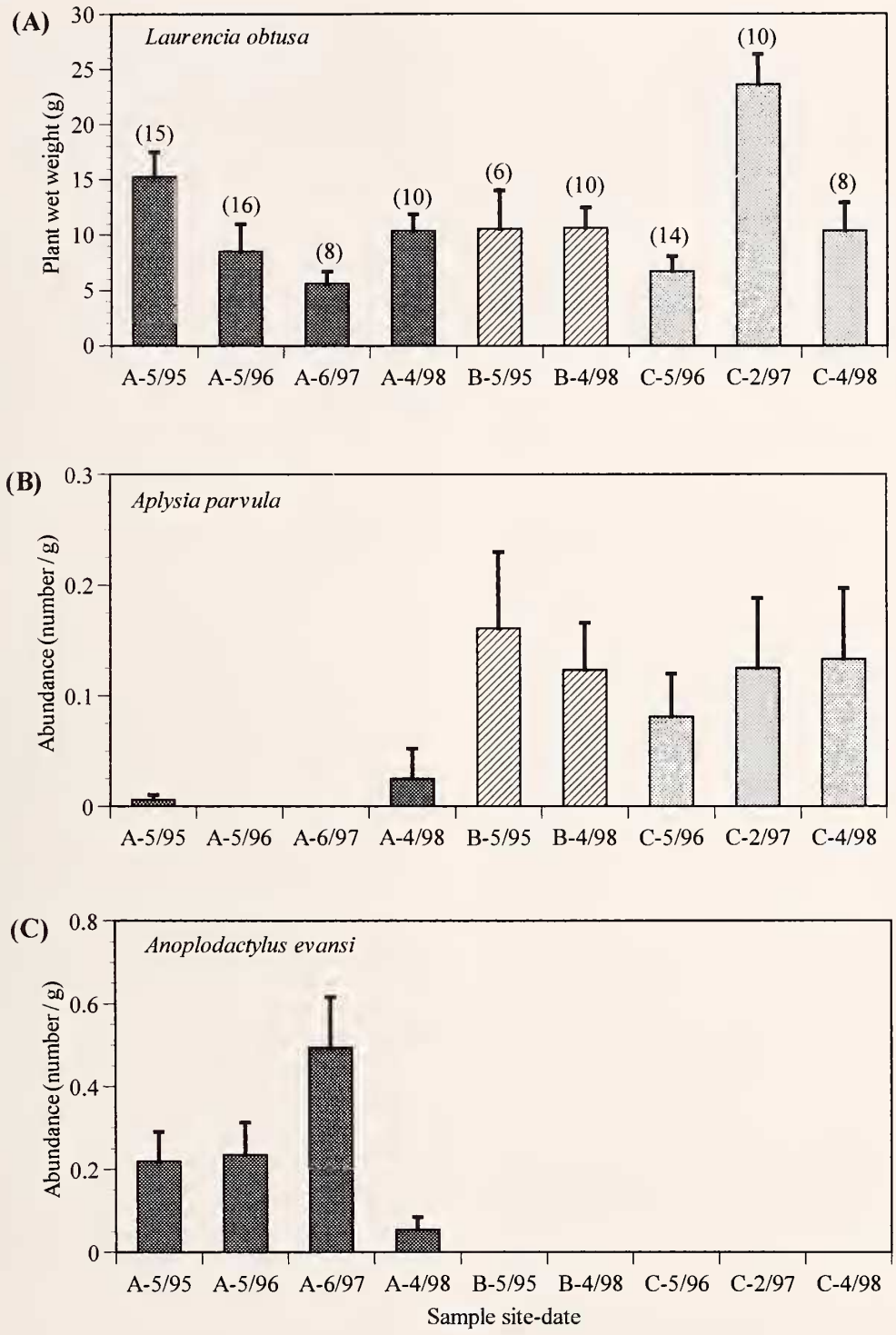

Figure 4

(A) Mean size of *Laurencia obtusa* (g ww) + 1SE at sampling sites in Port Jackson. Samples identified by site letter and sample date (month/year). Number of plants per sample is shown in brackets above bars, (n). (B) Abundance of *Aplysia parvula* on *Laurencia obtusa* (number of sea hares/g ww) + 1SE at sampling sites in Port Jackson. (C) Abundance of *Anoplodactylus evansi* on *Laurencia obtusa* (number of pycnogonids/g ww) + 1SE at sampling sites in Port Jackson.

Table 2

Analysis of variance comparing: (A) thalli size of *Laurencia obtusa* at sites in Port Jackson, and (B) the abundance of *Aplysia parvula* on *L. obtusa* (Ln(x + 1) transformed) at sites in Port Jackson. Sampling dates were pooled for each site in analyses. The results of a Tukey's HSD test showed the abundance of *Aplysia parvula* at site A was significantly different ($\alpha = 0.05$) from sites B and C.

Source of variation	Species					
	(A) *L. obtusa*			(B) *A. parvula*		
	df	F	*P*	df	F	*P*
Between groups	2	0.85	0.429	2	13.44	< 0.001
Within groups	94			94		

thobranchs, including the nudibranchs *Bornella stellifer, Austraeolis ornata* Angas, 1864, and *Spurilla australis* Rudman, 1982, not just the cerata as was observed for *Anoplodactylus carvalhoi* (Piel, 1991). The digestive gland of some sea hares was not eaten by *A. evansi. Aplysia parvula* stores the bulk of acquired algal secondary metabolites in its digestive gland (de Nys et al., 1996), so pycnogonids would avoid exposure to high concentrations by rejecting this organ. Only small opisthobranchs less than 300 mg were eaten, as larger animals could not be subdued, indicating an effect of prey body size. Pennings (1990a) also found an effect of prey body size on the capture success of opisthobranchs by *Aglaja inermis* Cooper, although in this instance, smaller individuals were consumed less often because habitat complexity aided predator evasion. Group feeding by *A. evansi* may facilitate (by weight of numbers) successful attacks on opisthobranchs larger than the prey size range found here. The nocturnal vertical movement of *A. parvula* (Rogers et al., 1998) and nocturnal activity of *A. evansi* may also increase the encounter rate between predator and prey in this system.

The local distribution of *Anoplodactylus evansi* was restricted, with pycnogonids found only at one of four nearby sites that had similar benthic communities (Figure 1). *A. evansi* has been collected at several sites along the New South Wales coastline, and as far south as Tasmania (Clark, 1963), so its limited distribution in Port Jackson contrasts with its wide distribution along the adjacent coastline. The limited distribution of this pycnogonid is most probably due to its brooding reproduction (King, 1973), and consequent limited dispersal to nearby seaweed. At site A, where *A. evansi* was found, pycnogonids occurred on several different seaweeds and a bryozoan, indicating that a broad range of organisms is used as habitat.

Natural levels of secondary metabolites and other diet-derived defenses of the opisthobranch mollusks investigated here had no effect in deterring *Anoplodactylus evansi* from attacking and consuming them. The small opisthobranchs consumed by *A. evansi* may lack sufficient quantities of such compounds to form an effective deterrent, although some juvenile sea hares can have high concentrations of secondary metabolites (Rogers, unpublished data). Artificially increasing the levels of metabolites present to double their average quantity did deter *A. evansi* from feeding on juvenile *Aplysia parvula,* demonstrating a quantitative deterrent effect. A possible reason why *A. evansi* did not consume all sea hares (< 300 mg ww) offered to them (see Figure 2) may be because the rejected sea hares had higher levels of secondary metabolites. Hence, concentration of metabolites can reduce feeding by *A. evansi,* but most *A. parvula* outgrow the prey range of this pycnogonid before they can store the levels of metabolites necessary for deterrence. A similar process may occur for the other opisthobranchs investigated, except for the ascoglossans, which attain much smaller maximum sizes (Table 1).

The abundance of *Aplysia parvula* was significantly lower on the red alga *Laurencia obtusa* at site A over consecutive years compared to other nearby sites where *Anoplodactylus evansi* did not occur. *L. obtusa* thalli from site A were similar in size to thalli at the other sites sampled. *L. obtusa* thalli inhabited by *A. evansi* were observed to persist into the winter, whereas thalli at other sites disappeared. The disjunct distribution of the pycnogonid *A. evansi* and sea hare *A. parvula* is consistent with this predator excluding *A. parvula* from site A, although other explanations are possible.

Anoplodactylus evansi is able to tolerate low levels of secondary metabolites and feed successfully on a wide variety of small opisthobranchs with different defensive substances. The opisthobranchs investigated here are known to sequester different metabolites (Gunthorpe & Cameron, 1987; Avila, 1995; de Nys et al., 1996), and the juvenile *Aplysia parvula* tested here contained secondary metabolites from *Laurencia obtusa* or *Delisea pulchra,* but all were consumed nonetheless. The presence of "novel" secondary metabolites from *D. pulchra,* which did not co-occur with *A. evansi* in Port Jackson, suggests that this pycnogonid can tolerate a variety of secondary metabolites in its diet. Given the wide range of opisthobranchs eaten by *A. evansi* in this study, such compounds may also include those found in sponges, cnidarians, bryozoans, and other dietary items of the opisthobranchs. One reason this pycnogonid can feed successfully on potentially poisonous opisthobranchs could be their digestive processes involving pinocytosis and intracellular digestion of food particles (Richards & Fry, 1978). Isolation of prey tissue containing secondary metabolites in vacuoles by pycnogonids, with eventual excretion of the residual body and presumably any toxins, would render such substances harmless. Disposal of sec-

ondary metabolites by this digestive process may also account for the trace amounts of compounds found in *A. evansi* which had consumed *Aplysia.* The pycnogonid *A. evansi* is thus a generalist predator of opisthobranchs, which may overcome their defenses by virtue of an isolating digestive process and by consuming small individuals which may lack substantial quantities of diet-derived defenses.

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